

**CHRYSOMYA MEGACEPHALA (FABR.) IS
MORE RESISTANT TO ATTACK BY
CH. RUFIFACIES (MACQUART) IN A
LABORATORY ARENA THAN IS
COCHLIOMYIA MACELLARIA (FABR.)
(DIPTERA: CALLIPHORIDAE)**

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Abstract.—*Chrysomya* Robineau-Desvoidy blow flies recently introduced to the Americas include two species, *Ch. megacephala* (Fabr.) and *Ch. chloropyga* Wiedemann (= *Ch. putoria*) with purely saprophagous larvae, and two, *Ch. albiceps* (Wiedemann) and *Ch. rufifacies* (Macquart), that are facultative predators on other maggots. Patterns of adult abundance suggest that the invading species suppress the saprophagous native *Cochliomyia macellaria* (Fabr.), and do so more effectively in combination than individually. We hypothesized that *Ch. megacephala*, historically sympatric with *Ch. rufifacies*, is relatively resistant to predation by *Ch. rufifacies*, which could provide it with a competitive advantage over a more vulnerable *C. macellaria* when larvae of all three occur together. To test this hypothesis, larvae of both prey species were individually paired with larvae of *Ch. rufifacies* in the laboratory. *C. macellaria* were consistently killed at a higher rate than were *Ch. megacephala*.

Key Words.—Insecta, biological invasion, introduced species, competitive displacement, higher-order interaction, carrion, blow fly

Old World blow flies in the genus *Chrysomya* Robineau-Desvoidy have been spectacularly successful following their recent invasion of the Western Hemisphere. Introduced at two locations in the mid 1970's, *Ch. albiceps* (Wiedemann), *Ch. chloropyga* Wiedemann (= *Ch. putoria*) and *Ch. megacephala* (Fabr.) in Brazil (Guimarães et al. 1979) and *Ch. rufifacies* (Macquart) in Costa Rica (Jirón 1979), they quickly became widespread and abundant in Latin America (Baumgartner & Greenberg 1984, Baumgartner 1988, Mariluis & Schnack 1989, Olsen et al. 1992., J. Mendez L., pers. comm., Kurahashi et al. 1994). Within two decades, *Ch. rufifacies* and *Ch. megacephala* had spread far enough to be firmly established at locations in the southern USA (Wells 1991, Baumgartner 1993), and *Ch. chloropyga* occurs as far north as Panama (J. Mendez L., personal comm.).

Chrysomya chloropyga and *Ch. megacephala* are typical synanthropic pests, with saprophagous larvae usually found in carrion or feces (Greenberg 1971, Laurence 1986). *Chrysomya albiceps* and *Ch. rufifacies*, so similar to each other in form and natural history that their status as separate species has been debated (Tantawi & Greenberg 1993), have larvae that eat both carrion (and rarely live flesh) and other maggots (Fuller 1934, Ulyett 1950). The latter two species are also distinguished by the presence of prominent spiny tubercles (Fig. 1), which we believe serve to reduce cannibalism.

As *Chrysomya* densities in the New World have increased, sympatric popula-

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Figure 1. Larva of *Chrysomya rufifacies* (with tubercles) attacking a larva of *Phormia regina* (Meigen). The head of *C. rufifacies*, inserted into the other larva, is down in this view.

tions of the native calliphorid *Cochliomyia macellaria* Fabr. have decreased, sometimes precipitously, and this has been interpreted as competitive displacement (Guimarães et al. 1979, Baumgartner & Greenberg 1984, Wells & Greenberg 1992, Paraluppi & Castellon 1994). A similar decline may be happening to *Lucilia exima* (Wiedemann) (Baumgartner 1993). Competition for food between carrion-fly larvae is often intense (Hanski 1987). Because the invaders don't seem to be filling any previously unexploited niche, i.e., they are eating the same carrion and feces that are already exploited by native flies, the ability to out-compete native species seems necessary for the success of *Chrysomya* in the Americas.

Some evidence indeed suggests that the *Chrysomya* spp. have a stronger negative effect on *Co. macellaria* in combination than individually. At a site in Peru where *Ch. chloropyga* became common but *Ch. albiceps* was rare, *Co. macellaria* dropped during a 4-year period from 46% to 11% of the adult population at baits, while at a site where both invaders were common, reduction of the native fly was from 89% to 0.2% (Baumgartner & Greenberg 1984). At Brazilian locations where all three *Chrysomya* are abundant, the previously common *Co. macellaria* has been described as rare or absent (Guimarães et al. 1979, Paraluppi & Castellon 1994). *Ch. rufifacies* is the only member of the genus known to be established in Texas, and although it was experimentally shown to reduce the number of *Co. macellaria* bred from carrion, the native fly is still abundant (Wells & Greenberg 1992, 1994).

The advance of these flies is in contrast to previous (and separate) introductions to Latin America of *Ch. megacephala*, *Ch. chloropyga* and *Ch. rufifacies* that failed (Baumgartner & Greenberg 1984, Baumgartner 1993). It is rather difficult to determine why an invasion did or did not succeed, but we hypothesize that the appearance of several *Chrysomya* spp. at the same time at least contributed to their successful establishment. Others have observed that coevolved sets of introduced species can be more able to invade because they have a greater impact on the invaded community than would be predicted from their individual interactions with native organisms (Simberloff 1991). In the case of *Chrysomya*, this would occur if the purely saprophagous larvae are adapted to resist or avoid the attack of their predaceous congeners with which they have long been sympatric. *Chrysomya megacephala* or *Ch. chloropyga* would then be more likely to successfully invade if *Ch. albiceps* or *Ch. rufifacies* were also present.

Chrysomya megacephala is commonly found with *Ch. rufifacies* in the Oriental, Australasian and Oceanic regions (James 1977, Kurahashi 1989). In addition, its successional position within carrion is similar to *Co. macellaria* (making them almost certainly competitors for the same food), and both are species attacked by *Ch. rufifacies* in the field (Bohart & Gressitt 1951, Wells & Greenberg 1994). In this study, we measured the rate of predation by *Ch. rufifacies* larvae on *Ch. megacephala* and on *Co. macellaria* in a laboratory arena.

METHODS AND MATERIALS

All larvae used were third instars approximately one cm in length. During a trial, 20 *Co. macellaria* and 20 *Ch. megacephala* were individually paired with a single *Ch. rufifacies* (40 total) within a 60 × 15 mm plastic petri dish. Dishes were arranged in a 5 by 8 pattern on a laboratory shelf, with alternating prey species in place. A trial began when a *Ch. rufifacies* larva was quickly dropped

Table 1. Number of *Cochliomyia macellaria* and *Chrysomya megacephala* larvae, out of a total of 20 each, successfully attacked by *Chrysomya rufifacies*.

Trial	<i>Co. macellaria</i>	<i>Ch. megacephala</i>
1	18	15
2	18	14
3	18	14
4	5	2
5	17	16
6	9	6

into each dish. After 20 min at 25 C, all larvae that, based on our experience, were damaged enough to be fatally wounded were counted. These included larvae that were shriveled, had body contents extruded through a hole in the cuticle, or were in the grip of a feeding *Ch. rufifacies*. Six trials were performed, each with a new generation of larvae.

Larvae were obtained from two sets of fly colonies. For trials 1–4 these were: *Co. macellaria* from Kerr County, TX, USA, colonized for an unknown number of generations; *Ch. megacephala* and *Ch. rufifacies* from Yona, Okinawa, Japan, colonized for 3–10 generations. Colonies for trials 5 and 6 were: *Co. macellaria* from W. Lafayette, IN, USA, colonized for 4–5 generations; *Ch. megacephala* from Kimbe, New Britain, Papua New Guinea, colonized for 10–11 generations; *Ch. rufifacies* from Matsuda, Okinawa, Japan, colonized for 3–4 generations.

RESULTS AND DISCUSSION

In every trial, *Ch. rufifacies* killed or wounded a greater number of *Co. macellaria* than *Ch. megacephala* (Table 1). Under these conditions, *Ch. megacephala* was more resistant to attack by its historically sympatric congener than was the previously allopatric *Co. macellaria* (sign test, $p = 0.03$). From casual observation, we believe that *Ch. megacephala* was more quick to struggle vigorously and flee following contact with the mouthparts of *Ch. rufifacies*, although no effort was made to quantify such behavior.

Although the total number killed per trial varied from 7 to 33, the relative difference between the two prey species was similar for all trials. We suspect that each batch of *Ch. rufifacies* had a particular "hunger level" that influenced the overall probability and/or strength of attack, but that had no influence on the relative vulnerability of prey species.

These results, albeit produced in a highly artificial setting, support the hypothesis that *Ch. megacephala* is a stronger competitor against *Co. macellaria* when *Ch. rufifacies* is present. To the extent that our observations apply to wild populations, it follows that the establishment and spread of *Ch. megacephala* within the range of *Co. macellaria* was aided by the presence of *Ch. rufifacies* or the nearly identical *Ch. albiceps*. Further experimental manipulations and field observations are needed to confirm this complex interaction.

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